Fluctuations in coral health of four common inshore reef corals in response to seasonal and anthropogenic changes in water quality

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Abstract

Environmental drivers of coral condition (maximum quantum yield, symbiont density, chlorophyll *a* content and coral skeletal growth rates) were assessed in the equatorial inshore coastal waters of Singapore, where the amplitude of seasonal variation is low, but anthropogenic influence is relatively high. Water quality variables (sediments, nutrients, trace metals, temperature, light) explained between 52 to 83% of the variation in coral condition, with sediments and light availability as key drivers of foliose corals (*M.ampliata, P.speciosa*), and temperature exerting a greater influence on a branching coral (*P.damicornis*). Seasonal reductions in water quality led to high chlorophyll *a* concentrations and maximum quantum yields in the corals, but low growth rates. These marginal coral communities are potentially vulnerable to climate change, hence, we propose water quality thresholds for coral growth with the aim of mitigating both local and global environmental impacts.

Keywords: Coral photo-physiology, coral growth, turbid reefs, water quality, sediments, tolerance, Singapore

1. Introduction

Over one third of the world's coral reefs are situated in South East Asia and they host some of the highest levels of marine biodiversity on Earth (Burke et al., 2002). They are also threatened by human activities including over exploitation, coastal development and pollution (Bryant et al., 1998; Burke et al., 2002). Singapore's coral reefs, home to 255 hard coral species, lie within the port limits of one of the world's busiest harbours (Huang et al., 2009). Land reclamation and the amalgamation of reef-fringed islands for port construction and oil refineries have resulted in a loss of over 60% of Singapore's original reef area (Chou, 2006). Ongoing coastal development and dredging of shipping channels, which release large volumes of sediments, associated nutrients and trace metals into the marine environment, are primary threats to coral reef health in Singapore (see review in Todd et al., 2010).

Singapore's coral reefs are dominated by sediment-tolerant coral taxa which are generally restricted to the upper 5 m of the reef slope due to low light levels (Huang et al., 2009; Tun et al., 1994). Sediment loads can stress corals both in suspension, which increases turbidity and limits light penetration (Rogers, 1990; Wolanski and De'ath, 2005), and when deposited (Lui et al., 2012). Limited light penetration reduces photosynthesis and energy production by the symbiont algae within the coral (Anthony and Connolly, 2004; Falkowski et al., 1990), whereas deposited sediments may smother corals (Loya, 1976), reduce hard substrate availability thereby limiting larval settlement (Fabricius et al., 2003), and increase the prevalence of tissue infections (Bruno et al., 2003). Some species have developed morphological and/or physiological mechanisms to cope with increased sediment loads, which allow these corals to survive, and in some cases dominate, coral reefs exposed to sediments (Erftemeijer et al., 2012). For example, foliose corals such as *Turbinaria* develop funnel shapes which channel and concentrate sediments to central regions of the colony thereby limiting the surface area affected by sedimentation (Sofonia and Anthony, 2008). Other corals such as *Goniastrea* are known to increase their heterotrophic feeding capabilities in response to limited light (Anthony, 2000). Despite limited coral growth at depth due to high light attenuation and high sedimentation rates (Dikou and van Woesik, 2006; Lane, 1991; Low and Chou, 1994), there is recent evidence that coral cover and biodiversity in Singapore's shallow waters has not changed over the last ~25 years (Tun, 2013). These data suggest that local corals may have reached equilibrium with contemporary water quality conditions, considered by many to be marginal for reef growth (Browne et al., 2012).

Despite being potentially resilient, coral reefs in Singapore may be surviving at the edge of their environmental tolerances and therefore be more vulnerable to the effects of climate change. At present, there are no long-term in situ data that document how local corals respond to environmental conditions, including fluctuations in sediment loads and water quality. Such a data set would provide key information on coral condition in Singapore in response to environmental fluctuations, improve current understanding on how these corals have adapted and/or acclimated to marginal reef growth conditions, and address concerns on reef vulnerability to climate change. Variations in coral condition and physiology with light (Falkowski et al., 1990; Hennige et al., 2008; Hennige et al., 2010) and temperature (Anthony and Connolly, 2007; Coles and Jokiel, 1977; Crabbe, 2007; Fagoonee et al., 1999) are well documented, but long-term studies (>6 months) of coral condition that cover a substantial spatial area (>1 km) and measure a number of key environmental drivers, are rare. Notable exceptions include: Hennige et al. (2010) who documented changes in community composition, coral metabolism and symbiodinium community structure along environmental gradients in Indonesia; Fagoonee et al. (1999) who monitored symbiont density in *Acropora* in the field for over 5 years in response to light, sea water temperatures and seasonal changes in nutrient concentrations; Fitt et al. (2000) who measured tissue biomass and symbiont density for five hard coral species for up to 4 years, and Cooper et al. (2008) who found that variations in symbiont density were strongly associated with sea water temperatures and water quality. These studies all indicate that coral physiology and coral condition are influenced not only by light and temperature, but by seasonal and/or spatial variations in water quality. In Singapore, where the amplitude of seasonal environmental variation is low, water quality is the primary threat to the health and survival of corals. A comprehensive assessment of spatial and temporal variations in water quality with coral condition would further current understanding of local coral responses and reef resilience.

Two key aspects of water quality that have received the most attention in recent years are sediments and nutrient loads. A review of the impacts of sediments on coral reefs by Risk and Edinger (2011) summarises research findings in this field to date and provides key indicators of sediment stressed reefs, which include low species diversity and live coral cover, low coral recruitment rates, high Ba/Ca ratio in coral skeleton as well as high coral extension rates but low skeletal densities. High nutrient loads on coral reefs were also found to lead to changes in coral growth with high levels of nitrogen resulting in stunted growth whereas high levels of phosphorus caused increased linear extension but declines in skeletal density (Koop et al. 2001). The combined effects of high sediments and nutrients have been less well researched, although they are thought to act antagonistically: with sediments typically stunting coral growth and nutrients increasing growth (Edinger and Risk 1994; Edinger 2000). In a recent review by Risk (2014) a range of assessment techniques to determine sediment and nutrient stress on reefs are identified which include the use of $\delta^{15}N$ in coral tissue (Risk et al. 2009). This promising retrospective technique is, however, relatively new and requires more extensive testing under different environmental scenarios.

In the present study, we analyse four parameters of coral health in relation to fluctuations in nutrient and sediment loads. We measured coral photo physiology (maximum quantum yield, symbiont density and chlorophyll *a* content) as well as coral growth rates. These indicators of coral health allowed to follow changes over shorter sampling periods (non-retrospective) and test the effects of seasonal fluctuations in water quality. Specifically, the objectives of the paper were to: 1. Assess spatial and temporal variations in coral conditions, 2. Identify key environmental drivers of coral condition, and 3. Identify water quality threshold values for coral growth in Singapore's coastal waters.

2. Materials and Methods

2.1 Study species and field sites

In February 2012, three colonies of *Merulina ampliata*, *Pachyseris speciosa* and *Platygyra sinensis* were collected from three sites around Singapore (Kusu Island, Pulau Hantu, Labrador Park; Fig. 1) at 3 to 4 m depth at Lowest Astronomical Tide (LAT). In addition, three colonies of *Pocillopora damicornis* were also collected from Kusu Island. These corals were selected as they represent both abundant (>5% cover), resilient species (e.g. *M.ampliata*) and rarer, sensitive species (e.g. *P.damicornis*), as well as range of coral morphologies. Each colony was broken into fifteen fragments (approximately 5 cm × 5 cm), and mounted either on to a plastic grid or wall plug (for *P.damicornis*) using underwater epoxy resin (Epoputty, UK). Once the resin had hardened, all coral fragments at each site (a total of 135 fragments each at Pulau Hantu and Labrador Park, and 180 fragments at Kusu Island) were secured onto a frame positioned on the reef slope at 3 m. Following a one month recovery period, two thirds of the coral fragments were removed from each site with one third going to each of the other two sites. This reciprocal transplantation resulted in each site having five fragments of the same nine genotypes for *M.ampliata, P.speciosa* and *P.sinensis* and three genotypes for *P.damicornis.* Coral fragments remained in situ for one year and health was monitored monthly after a one month acclimation period from April 2012 to March 2013.

The three field sites in Singapore are characterised by different sedimentary regimes, exposure to natural waves, and anthropogenic influences including ship wakes and dredging activities. Turbidity and light at Kusu Island (at 3 m LAT; N 1.22838, E 103.85525), the most eastern and exposed site, typically ranged from 1 to 3.0 mg l^{-1} with maximum peaks reaching 40-50 mg l^{-1} and 50 to 400 PAR (photosynthetically active radiation), whereas Pulau Hantu, the most sheltered westerly site (N 1.22640, E 103.74675), had lower maximum peaks (20-30 mg l^{-1}) and higher light penetration (100 to 500 PAR). The third site at Labrador Park is situated next to the mainland, approximately 500 m east of a land reclamation site and busy harbour (N 1.26636, E 103.80015). During 2012, this site was influenced by dredging near the land reclamation site as well as ship-wakes from fast moving ferries (pers. Obs.). Consequently, turbidity levels typically ranged from 5-20 mg l^{-1}, with maximum peaks reaching >150 mg l^{-1} and light levels were lower (0 to 300 PAR) compared to Kusu Island and Pulau Hantu.

2.2 Environmental variables

Temporal variations in water quality, sediment accumulation rates (SAR), light penetration and sea surface temperature (SST) were collected twice each month. Water quality parameters included chlorophyll *a*, suspended sediment concentration (SSC), alkalinity, ammonia (NH_3), nitrate (NO_3), phosphate (PO_4), silicates, total nitrogen (TN), total phosphate (TP) and trace metals (aluminium, silver, cadmium, copper, iron, nickel, lead, and zinc). Water samples (5 L) were collected by divers next to the floating frames at 3 m at

LAT. For chlorophyll *a*, triplicate water samples (250 ml), stored in dark bottles during transportation, were filtered through pre-combusted glass fibre filters (25 mm, nominal pore size 0.7 µm) and stored at 4°C. Concentrations of chlorophyll *a* were determined using a fluorometer (Turner Designs 7200-000 with Trilogy Module 7200-046, USA), following a 24 h dark extraction in 90% acetone at 4°C, and the equations of Jeffrey and Humprey (1975). SSC concentrations were determined from triplicate water samples (1 L) which were filtered through weighed standard filter paper (47 mm, nominal pore size 1.5 µm). The residue retained on the filtered paper was dried to a constant weight at 103°C. The alkalinity of the water was determined from three unfiltered replicates (50 ml) using an auto-titrator (Mettler Toledo T70, Switzerland) and 0.1 N sulphuric acid in accordance with the APHA 2230 B standards. A flow injection analyser (SKALAR SA5000, Netherlands) and methods described by Ryle et al. (1981) was used to determine the concentrations of ammonia, nitrate, phosphate and silicate from three filtered 40 ml replicates. Levels of total nitrogen and phosphate (3 × 40 ml), following oxidation (persulfate) and digestion (boric acid), were also determined using a flow injection analyser in accordance with the APHA 4500 standards, and trace metal analysis (3 × 40 ml) was carried out on an Inductively Coupled Plasma (ICP) mass spectrometer (Thermo Scientific, Germany) in accordance with the APHA 3125 B standards. All APHA standards followed protocols outlined in the 'Standard methods for the examination of water and wastewater' (Rice et al., 2012).

Sediment accumulation rates were assessed using three replicate sediment traps (5 cm diameter × 25 cm length) at each site which were positioned on the side of the frame at the same height as the coral fragments, approximately 50 cm off the sea bed (Storlazzi et al., 2011). Sediments in the traps were collected each month, dried and weighed (mg cm^{-2} d^{-1}). Sediment particle size was determined using a laser diffraction particle size analyses

(Malvern Mastersizer Particle Size Analyser, UK). Light penetration (PAR; µmol photons m^{-2} s^{-1}) was recorded using the Diving-PAM fluorometer during 10:00 h to 12:00 h whilst monitoring the maximum quantum yield, and also by light loggers (Odyssey, New Zealand) that were deployed at each site (up to three weeks per deployment) throughout the year. Due to sediment settling on the Odyssey light sensor, it was not possible to leave the sensors in situ for longer periods of time. SST data was also collected during the coral condition monitoring by the Diving PAM fluorometer to give 'on the spot' temperature data rather than continuous data. These data were aligned with satellite imaging data collected by the Singaporean Meteorological Services at the water surface. The total accumulated monthly rainfall data was also obtained from the Singaporean Meteorological Services.

2.3 Coral condition

Four physiological parameters were monitored throughout the year in the assessment of coral condition. Parameters included the maximum quantum yield (Fv/Fm), skeletal growth rates (cm^2 mon^{-1}), symbiont density (number cm^{-2}) and chlorophyll *a* (µg cm^{-2}). The maximum quantum yield, measured monthly (except during July and September 2012) and growth rates, quantified approximately every two months when visibility would allow, were determined from three out of the five replicate coral fragments from each genotype. Samples for symbiont density and chlorophyll *a* analysis were collected from the remaining two fragments in April, June, August and October 2012, and February 2013.

F_v/F_m was measured in situ using a Diving-PAM (Walz, Germany) between the hours of 10:00 h and 12:00 h. Coral colonies were covered for 20 min to maximise the frequency of the open photosystem II reaction centres (Winters et al., 2003). The fluorometer's optical-fibre probe was kept at a constant distance of 5 mm from the surface of the coral and the average of five measurements for each coral fragment was calculated. F_o was measured by applying a pulsed measuring beam of <1µmol photon m^{-2} s^{-1} and the emission F_m was measured following the application of a saturating pulse of actinic light (>1000 1 µmol photon m^{-2} s^{-1}).

The two-dimensional surface area was assessed from photographs, analysed using CPCe software (NOVA, USA), to determine the monthly skeletal growth rates. The skeletal growth rate is given as a surface area (cm^2 mon^{-1}) for all coral species except *P.damicornis* whose growth rate was assessed as the average linear extension rate of five tagged branches (cm mon^{-1}) per fragment. Two dimensional surface areas were adjusted to account for variations in surface topography by using a rugose ratio derived with the paraffin wax method applied to 10 samples of *M.ampliata, P.speciosa* and *P.sinensis* (Stimson and Kinzie, 1991). There are several additional parameters that can be used to measure coral growth rates that include linear extension rates, skeletal density, and calcification rates (Browne 2012). The latter two techniques are, however, destructive and cannot be applied here given that the same coral fragments needed to be reassessed each month. Surface area measurements also allowed for comparative analyses between different coral morphologies and could be easily incorporated into monitoring programmes. Furthermore, a recent review of the biology and economics of coral growth rates found that surface area are best determinants of coral growth (and biomass) for both plate and massive corals (Osinga et al. 2011).

Coral samples collected for symbiont density and chlorophyll *a* analysis were transported in ziplock bags kept in the dark on ice packs. Samples were stored at -20°C prior to processing. The method for the estimation of symbiont density and chlorophyll *a* concentrations followed Ben-Haime et al, (2003) and the equations of Jeffrey and Humphrey (1975).

2.4 Water quality thresholds

Water quality thresholds were calculated based on variable coral growth rates. Coral growth rates were selected as the key indicator of water quality as growth represents the outcome of several processes including photosynthesis and heterotrophy. We calculated the mean annual percentage growth rate for each coral species, and compared it to the mean monthly growth rate. Water quality parameters during months where the percentage deviation in growth rate was >15% below the mean, were considered to be above critical thresholds for coral growth, and those where the percentage deviation in growth was >15% above the mean, were considered to be below critical thresholds for coral growth. The standard error (SE) of yearly growth rates for each coral species ranged from 14-18% of the mean yearly growth rate. Hence, a 15% threshold value was selected as this allowed for natural variability in coral growth measured over the year.

2.5 Statistical analysis

Data on coral condition for each genotype for each species were averaged from three replicates for yield and coral growth rates, and from two replicates for symbiont density and chlorophyll *a* concentrations. Data were checked for normality and homogeneity of variance using the Shapiro-Wilk test and Levene's test respectively. One-way repeated measures ANOVA were performed, with adjustments made for multiple comparisons using Bonferroni corrections, to assess if and when there was a significant difference in coral condition among sites over time. Mauchy's test of sphericity was carried out and, where the assumption was violated, data were adjusted using the Greenhouse Geisser adjustment. Post hoc analyses using Bonferroni corrections indicated between which sites significant differences occurred.

Monthly variations in water quality variables were averaged over five sampling periods (April 2012, May-July 2013, August –October 2012, November 2012-January 2013, February-March 2013). These sampling periods were synchronised with the monsoonal seasons in Singapore which are characterised by variations in SST and rainfall data.. A water quality index (WQI) was calculated using the sum of the Z score transformation ($x=0$, $\sigma=1$) for water quality variables (ammonia, nitrate, total nitrogen, phosphate, total phosphate, silicate, trace metals, chlorophyll *a*, suspended sediments) following Cooper et al (2007). A negative score indicates low nutrient, clearer waters whereas a positive score indicates high nutrient, more turbid waters. Coral growth rates were log-transformed and compared between months with improved WQI (<-0.10) and poor WQI (>0.00) using a paired T-test.

PCA was used to examine the relationship between spatial and temporal variations in environmental variables over one year (2012/2013). Data were log-transformed before PCA, and results summarised in a bi-plot containing the distribution of environmental parameters in a two-dimensional space. To investigate key environmental driving factors of coral condition, a Distance Linear Model (PERMANOVA) was performed using a stepwise additional of environmental variables. Seasonal mean values for each coral condition variable were square root transformed and a resemblance matrix was created using Bray Curtis similarity index. The model was able to identify which combination of variables explained the most variation in coral condition for each coral species across all three sites. The statistical analysis was carried out using the statistical software packages RStudio (version 0.98.507) and PRIMER 6 (version 6.1.16).

3. Results

3.1 Environmental variables

3.1.1 Rainfall and water temperature

The total monthly rainfall (supplied by the Singapore Meteorological Service) was consistent with previous years with March (~100 mm) and June (~50 mm) as the driest months. The wettest months occurred at the end of the year (December) and midway through the year (April-May) when >300 mm rainfall per month was recorded (Fig. 2). SSTs were also consistent with previous years with a large peak occurring in May to June 2012 (~29.5^{o}C) and a smaller peak occurring in October to November 2012 (~29^{o}C). Lowest SSTs were recorded during January to February 2013 (~28^{o}C; Fig. 2). SSTs measured on the reef slope were lower than SST taken at 0 m, ranging from 26-28.5^{o}C, but followed the seasonal trends observed at the surface.

3.1.2 Spatial and temporal variation in water quality

The WQI was spatially and temporally variable with poor water quality typically observed at Labrador Park, and at all sites during the May to June 2012 period (Fig. 3). Poor water quality at Labrador was largely driven by an elevated WQI index value, attributed to high trace metal concentrations (aluminium >200 μg l^{-1}, iron > 100 μg l^{-1}, nickel >4 μg l^{-1}: Fig. 4), elevated suspended and deposited sediments (SSC > 10 mg l^{-1}, SAR < 37 mg cm^{-2} day^{-1}; Fig. 2) and reduced light levels (0 to 300 PAR; Fig. 2). Declines in water quality at all sites during May and June (season 2; Fig. 3) were attributed to elevated nutrient levels (NO_3 >200 μg l^{-1}, TN >200 μg l^{-1}; Fig. 5) as well as elevated sediment exposure and SST (>28 ^{o}C; Fig. 2 & 3). The WQI was most variable at Labrador Park (mean = 6.9), ranging from -4.13 to 24.27 (recorded in September 2012), contrasting with Pulau Hantu (mean = -3.97) where the WQI ranged from -9.30 to 8.65 (recorded in June 2012). Palau Hantu was typically characterised by courser sediments (median = 81 μm) and higher light levels (100-500 PAR; Fig. 3).

3.2 Coral condition

3.2.1 Maximum quantum yields

The maximum quantum yield varied significantly over the study period for all coral species (except *P.damicornis*), with yields typically peaking in June and November/December, and falling in October ($p<0.003$; Table 1 & Fig. 6). Yield also varied significantly between sites, with higher yields observed at Labrador Park ($p<0.05$; Table 2). Here, yields were also less variable over the year. Furthermore, there was a significant interaction between time and site for all coral species yields driven largely by higher and less seasonal variability at Labrador Park.

3.2.2 Growth rates

Growth rates varied over the year with higher growth rates occurring in April 2012 and February 2013 (Fig. 7), but were only significantly different over time for *M.ampliata* and *P.speciosa* (Table 1). Growth rates were not consistently higher or lower at certain sites (Table 2), except for *M.ampliata* and *P.sinensis* whose growth rates were significantly different among sites during specific months (e.g. higher growth rates observed at Hantu in April to May 2012; Fig. 7).

3.2.3 Symbiont densities and coral chlorophyll a concentration

There was no significant difference in symbiont densities and chlorophyll *a* among sites for all coral species ($p>0.05$; Fig. 8 & 9). Yet significant temporal differences in symbiont density were found for *M.ampliata* and *P.damicornis* ($p<0.017$, Table 1). In contrast, chlorophyll *a* concentrations varied significantly over the year for all coral species ($p<0.05$, Table 1).

3.2.4 Environmental drivers of coral condition

Water quality variables explained between 52 to 83% of the variation in coral condition over the study period (Table 3). Key drivers in coral condition varied between species with grain size having a significant influence on *M.ampliata* (67.6%), light and sediments significantly influencing *P.speciosa* (51.6%) coral health, and SST and sediments having the greatest influence on *P.damicornis* (82.9%; Table 3). No combination of water quality variables was able to significantly explain the temporal variation in *P.sinensis* condition over the year.

3.2.5 Water quality thresholds

The mean annual coral growth rates were 1.7 $\pm$ 0.3 cm^2 mo^{-1} (for *M.ampliata*), 3.1 $\pm$ 0.4 cm^2 mo^{-1} (for *P.speciosa*), 1.1 $\pm$ 0.2 cm^2 mo^{-1} (for *P.sinensis*), and 0.5 $\pm$ 0.1 cm mo^{-1} (for *P.damicornis*). Coral growth rates during months with poor WQI (>0.00) were significantly lower (p<0.05) than coral growth rates during months with improved WQI (<-0.10) for all coral species (Fig. 10). Months when the mean growth rate for all coral species fell by >15% included June (Z score = 7.92), September (Z score = 1.08) and December (Z score = 1.85). Water quality conditions during these months were considered to be over coral growth thresholds. In contrast, April (Z score = -4.09) and February (Z score = -3.56) had coral growth rates that exceeded the annual mean by >15%.

4. Discussion

The present study is the first to document temporal dynamics of coral photo-physiology and growth with seasonal environmental fluctuations in Asian equatorial waters. Light and temperature are key environmental cues frequently associated with temporal variations in coral photo-physiology (Piniak and Brown, 2009; Warner et al., 1996). However, at the equator ambient light and temperature are comparatively stable and, as such, the amplitude of seasonal environmental change is considered by many to be insufficient to provide reliable environmental cues for coral responses (Nieuwolt, 1973; Rinkevich and Loya, 1979). Nevertheless, previous work on Singapore reefs by Guest et al. (2005) demonstrated that corals displayed seasonal reproductive patterns and in the present study we found significant temporal and spatial variations in both water quality and coral condition. Labrador generally had lower water quality compared to Palau Hantu and Kusu Island, but all three sites experienced declines in water quality during the SW monsoonal period (May to June 2012). Seasonal fluctuations in rainfall influenced nutrient and sediment inputs, which in inshore waters are considered key drivers of coral condition (Cooper et al., 2008). This also appears to be the case in Singapore where coral condition during these months was relatively poor as evidenced by elevated yields and declining growth rates.

4.1 Seasonal and spatial environmental variation

Peaks and troughs in rainfall closely matched peaks and troughs in nutrient concentrations and sediment accumulation rates, suggesting that elevated rainfall rates and increased runoff into coastal waters result in elevated nutrient and sediment inputs. May and June had the highest nutrient (e.g. NO_3 >150 µg l^{-1}) and sediment inputs (SAR >15 mg cm^{-2} d^{-1}) whereas September and October were characterised by low rainfall (~100 mm mo^{-1}) and low nutrient inputs (e.g. NO_3 <100 µg l^{-1}). Elevated nutrient levels in May to July resulted in algal blooms and peaks in chlorophyll *a* concentrations from July to August. These months were also characterised by low nutrient concentrations, most likely due to algae removing nutrients from the water (Lapointe and Clark, 1992; Pastorok and Bilyard, 1985). It was during these months that trace metal concentrations increased. The increase in trace metal concentrations occurred with increased sediment suspension, suggesting that sediments were the primary source of trace metals.

Elevated and more variable fluctuations in SSC, trace metal and nutrient concentrations at Labrador Park are a consequence of the site's proximity to mainland Singapore, especially the associated coastal development and dredging projects. These anthropogenic impacts are known to increase sediment loads as well as resuspend bottom sediments, thus releasing nutrients and trace metals into the water column (Erftemeijer et al., 2012). Since November 2007, a large area (~2 km^2) of coastal waters, situated approximately 1 km to the west of Labrador Park, has been reclaimed for a port expansion. Elevated suspended sediment loads and trace metals were observed during periods of dredging activity and land in-filling. Nutrient concentrations were also typically higher at Labrador Park than at Pulau Hantu and Kusu Island, suggesting an inshore to offshore gradient in nutrient concentrations. Similar gradients have been observed within numerous coral reef systems in Asia (e.g. Hong Kong; Fabricius and McCorry, 2006) and in Australia (e.g. Great Barrier Reef; Cooper et al., 2007; Fabricius et al., 2008), and are driven by distance from the nutrient source and declines in hydrodynamic energy in protected bays close to shore which limit mixing and removal of nutrients.

In our study, of the seventeen water quality parameters measured monthly for one year, eight exceeded current water quality standards provided by both the Association of South-East Asian Nations (ASEAN) and the Australian and New Zealand Environmental and Conservation Council (ANZECC). Water quality parameters that exceed recommended trigger values included all the nutrients, chlorophyll *a*, turbidity, and copper (Table 5). Note that aluminium and iron levels were also elevated, but at present there is insufficient data on the impacts of these trace metals on biological organisms for standards to be set (ANZECC, 2000). Chlorophyll *a* and ammonia thresholds were exceeded at Kusu Island and Labrador Park for approximately 25% and 50% of the year, respectively. However, nitrate and TN thresholds were exceeded during 40 to 80% of the year, and phosphate levels were exceeded during 50 to 100% of the year, with consistently higher concentrations at Labrador Park. When water quality parameters are exceeded, limited light availability and high nutrient concentrations limit photo-trophic energy production and growth (Anthony and Hoegh-Guldberg, 2003), increase juvenile mortality rates (Loya, 1976; Rogers, 1983), and reduce coral recruitment (Fabricius, 2005). Lower coral fecundity has also been associated with elevated levels of copper [>2 $\mu g\ l^{-1}$; Reichelt-Brushett and Harrison (1999)]. At present, corals in Singapore are potentially stressed by elevated nutrient levels and trace metal concentrations, as well as sediments and associated reductions in light. Improving water quality may lead to increases in hard coral and phototrophic richness (De'ath and Fabricius, 2010), and mitigate the negative effects of climate change (Negri and Hoogenboom, 2011).

4.2 Environmental drivers of coral condition

Light is typically the primary driver of temporal variations in maximum photosynthetic yield, although SST has also been suggested as a key factor. Yields fluctuated most at Pulau Hantu, where light levels were also the most variable (100-500 PAR). In contrast, yields were elevated and stable at Labrador where light levels were consistently low (0-300 PAR). Few papers describe long-term changes in the photosynthetic capacity of corals in response to changing environmental conditions and, of those available, findings vary. Hill and Ralph (2005) did not identify any significant seasonal variations in the yield, whereas Warner et al. (2002) demonstrated that fluctuations in coral photosynthetic capacity in the Bahamas were strongly correlated with seasonal patterns of water temperature and light, with elevated yields during the cooler months when surface irradiance levels were high. Higher yields during cooler months have been noted elsewhere (Piniak and Brown, 2009; Warner et al., 1996), however, these trends are usually observed in regions characterised by intra-annual changes in temperatures regime. In the Bahamas, water temperature varied between 22°C to 34°C, whereas temperatures in Singapore are relatively steady (26-29°C). In contrast, Winter et al. (2006) found that seasonal variations in yields for corals in the Red Sea were related to light but not water temperatures. Exposure to high light levels (900-1,000 PAR) at 24°C and 31°C resulted in lower yields than at the higher temperature but at low light conditions (200-300 PAR). These data support our study, and suggest that light levels have a greater influence on coral yields than SST in equatorial regions.

Coral chlorophyll *a* concentrations have been observed to increase as water temperatures rise and light levels decline (Cooper et al., 2008) , as well as decrease with rising water temperatures (Fitt et al., 2000). The variable response with temperature is potentially due to the symbiodinium clade composition (Fitt et al., 2000). Different symbiodinium clades may vary physiologically, and certain clades are known to provide a physiological advantage to corals exposed to higher water temperatures (Berkelmans and Van Oppen, 2006). In the present study, high concentrations of chlorophyll *a* were measured in April 2012 in all species when SST peaked at >29°C. However, chlorophyll *a* concentrations were also higher at Labrador Park where light levels were consistently lower suggesting that in-water light levels were also a key driver of spatial variations in pigment concentration. Elevated chlorophyll *a* concentrations and associated yields would enable corals to maximise rates of photosynthesis under low light conditions frequently observed at Labrador Park.

Nutrient concentrations are also a key driver of coral condition (see review by Fabricius, 2005). There have been several studies that have documented the effects of elevated concentrations of nutrients on symbiont densities and chlorophyll *a* content (Hoegh-guldberg and Smith, 1989; Marubini and Davies, 1996; Szmant, 2002), photosynthesis (Kinsey and Davies, 1979) and coral growth (Ferrier-Page` s et al., 2001). Increases in symbiont density are typically associated with increases in Dissolved Inorganic Nitrogen (DIN = NO_3 + NO_2 + NH_4), whereas Dissolved Inorganic Phosphates (DIP = PO_4 + PO_3) have less of an effect (Fabricius, 2005). Symbiont density increases when DIN levels are enhanced, as this nutrient is preferentially used for symbiont growth over host tissue growth (Dubinsky and Jokiel, 1994). Marubini and Davies (1996) also found that chlorophyll *a* concentrations and symbiont densities increased with NO_3 levels, at concentrations comparable to that found in Singapore waters. In contrast, and in accordance with this study, both Ferrier-Pages et al. (2001) and Nordemar et al. (2003) found that nitrate concentrations had no effect on symbiont densities. These inconsistencies in symbiont responses between studies may, in part, be a result of environmentally unrealistic high levels of nutrients tested, but are most likely caused by a simplification of a complex natural system where the coral response is the outcome of several synergistic drivers. For example, symbiont densities which may increase with concentrations of NH_3 and NO_3 (Fabricius et al., 2005), have also been observed to decline at high turbidity (Costa et al., 2004; Li et al., 2008). If both environmental drivers increase concurrently, the outcome might result in no apparent influence on symbiont numbers.

Declines in growth rates in Singapore have previously been associated with elevated suspended sediments, light attenuation and nitrite-nitrate concentrations (Dikou, 2009). Our data supports this finding as lowest growth rates were reported at the site (Labrador Park) with the highest sediment loads, lowest light levels and highest nutrient concentrations. Furthermore, the mean growth rate of all coral species during months characterised by reduced water quality was significantly lower than in months when water quality had improved. These results also corroborate with research outside of Singapore. In Barbados coral growth rates (linear extension) correlated with a number of water quality parameters with suspended particulate matter as the best estimator of growth (Tomascik and Sander, 1985). Differences in growth rates response to water quality were also evident among coral species. The growth rate of *M.ampliata* and *P.speciosa*, the two fastest growing corals, varied significantly over time, suggesting that these corals are most sensitive to environmental fluctuations.

The variation in key environmental drivers of coral condition among species is most likely related to differences in morphology and physiological adaptations. Various aspects of the sediment regime (either SSC, SAR or grain size) explained significant proportions of the variation in coral condition for the three coral species (*M.ampliata, P.speciosa, P.damicornis* characterised by foliose morphology and/or small coral polyps (< 3 mm). *P.sinensis* has comparatively larger polyps and is considered to be more efficient at sediment removal (Stafford-Smith, 1993). Light availability was also an important driver of *P.speciosa* coral condition suggesting that this coral may be most sensitive to variations in light condition. All four coral species will most likely feed heterotrophically during low light conditions (Anthony, 2000), yet morphological differences may result in variable abilities to feed heterotrophically. Polyp projection and hetereotrophic feeding was observed in *P.sinensis* and *P.damincornis* fragments during the survey period, and *M.ampliata* (short tentacles) growth rates have previously been closely correlated with SSC in Singapore (Dikou, 2009). Interestingly, *P.speciosa* does not expand its polyps instead using its mesenterial feeders

(Stafford-Smith and Ormond, 1992). Lastly, *P.damicornis* has been closely linked to chlorophyll *a* content and SST, which is unsurprising given that this species is one of the most thermally sensitive corals (Jokiel and Coles, 1990).

4.3 Water quality thresholds for Singapore

In Singapore, where eight water quality thresholds were exceeded, seasonal variations and anthropogenic activities influence spatial and temporal differences in water quality and drive fluctuations in coral condition. Seasonal fluctuations in SST's and rainfall are relatively constant from year to year, and result in certain months that are more or less favourable for coral condition and growth. These environmental fluctuations also provide cues for processes such as reproduction, which typically occurs in April, following a rise in SST's and heavy rainfall (Guest et al., 2012a). It is, therefore, important that declines in water quality associated with anthropogenic activities do not occur during these sensitive months which would potentially negatively influence reproductive processes and hence the viability and longevity of coral reefs. Despite elevated nutrient levels, corals were healthy and growing, presumably because they have acclimated to these marginal reef growth conditions. There has been little variation in coral cover and diversity within shallow waters over ~25 years (<5 m; Tun, 2013) and corals were relatively tolerant to thermal stress following 2010 bleaching event (Guest et al., 2012b), which suggests that these corals are resilient to the negative effects of elevated sediment and nutrient loads. There is increasing evidence, however, that reduced water quality will exacerbate the negative effects of rising SST's due to global warming (Heiss, 1995; Meaney, 1973; Negri and Hoogenboom, 2011), and that government programs need to increase water quality to mitigate the effects of climate change.

At present, Singapore does not have any water quality thresholds or standards for inshore coastal waters. The first step for improving local water quality would be to set thresholds, specific to Singapore, based on long-term data sets that describe variations in organism and/or ecosystem health with fluctuations in water quality. Here we use coral growth rates as a measure of variations in coral health with water quality. Previous research would suggest, however, that coral growth is not a good measure of coral health. Brown et al. (1990) found that there was no detectible decline in coral calcification rates as a result of dredging while a more recent study in Indonesia found that there was a discrepancy between coral growth rates and declines in reef health (Edinger, 2000). Explanations for varying findings are potentially the result of different experimental designs and assessment methodologies. Other research used retrospective techniques which represent, at best, yearly averages of coral growth rates and, therefore, do not take into account short term fluctuations in coral health. Furthermore, previous studies have compared coral growth rates and reef health with changes in water quality from different sites (e.g. Edinger et al, 2000, Lapointe et al. 2010, Fabricius et al, 2005) rather than compared rates from the same sites over a relatively long timeframe. By comparing coral growth rates between sites there is the risk of incorporating additional environmental drivers that may influence coral health and there is less scope for identifying small fluctuations in coral health within sites. Results presented here indicate that coral growth rates are an appropriate indicator of water quality. Coral growth rates differ significantly between months characterised by low and high water quality, but are also closely follow fluctuations in coral photo-physiology. For example, high growth rates occurred during months when coral yields were reduced (Fig 6-9). Based on these considerations, water quality thresholds specific to Singapore were selected (explained in Materials and Methods), and compared to ANZECC and ASEAN standards (Table 5).

All nutrient thresholds for Singapore are above ANZECC and ASEAN thresholds, but note that the latter will be more conservative as they are based on several studies of additional organisms and marine ecosystems, and therefore represent thresholds for the protection of all aquatic life. Water quality thresholds stated here are for coral growth only. Thresholds provided include all the nutrients and turbidity levels. We have not considered thresholds for trace metals, given the complex interactions between trace metals, salinity, pH, temperature and water hardness, parameters which are known to affect trace metal toxicity (ANZECC, 2000). Yet, future water quality thresholds for Singapore will need to consider these given that many metals are toxic at high concentrations and can have detrimental influences on coral photo-physiology (Kuzminov et al., 2013) and reproduction. For example, elevated concentrations of copper (4.4 and 0.4 $\mu g\ l^{-1}$), comparable to that measured in Singapore, reduce the metamorphosis success of *Acropora millipora* larvae at higher temperatures (32^{o}C and 33^{o}C), thus exacerbating the effects of elevated SST's (Negri and Hoogenboom, 2011). These data reaffirm the importance of improving water quality for mitigating the impacts of global warming as well as preventing declines in water quality during warmer months when corals are already stressed.

5. Conclusions

This study represents the first year-long assessment of coral condition coupled with monitoring of a broad range of environmental variables in Singapore's inshore coastal waters, and illustrates the importance of water quality in driving coral condition in equatorial regions were the amplitude of seasonal variation is low. Monthly variations in rainfall, which influenced nutrient, sediment and light levels, were identified as key drivers of coral condition. In contrast, SST's had less of an influence on coral condition. Anthropogenic activities also had a discernible influence on water quality and coral condition, particularly at the site (Labrador Park) closest to the mainland, where chlorophyll *a* concentrations and yields were high, but growth rates were low. Even though Singapore hosts reefs that are apparently robust and resilient to low water quality levels, its corals may be more vulnerable to climate change than offshore reefs not influenced by poor water quality. Our results, and suggested water quality thresholds for coral growth, provide a critical starting point for the development of water quality guidelines for Singapore aimed to mitigate the effects of rising SST's due to climate change.

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Table 1: One-way repeated measures ANOVA using untransformed data (n=9, except for *P.damicornis* where n=3) to determine if there are significant differences in coral condition over time, and over time between sites for each coral species

Variable	**Species**	**Yield**				**Growth**				**Symbiont density**				**Chlorophyll *a***			
Time		**df**	**MS**	**F**	***p* value**	**df**	**MS**	**F**	***p* value**	**df**	**MS**	**F**	***p* value**	**df**	**MS**	**F**	***p* value**
	M.ampliata	3.9	0.025	8.83	**<0.001**	3.1	14.7	9.97	**<0.001**	2.1	5.01×10^{12}	7.65	**<0.001**	1.3	105.4	3.55	**0.050**
	P.speciosa	3.8	0.021	10.23	**<0.001**	3.5	18.2	8.69	**<0.001**	1.3	2.913×10^{12}	3.24	0.073	1.7	131.3	10.08	**<0.001**
	P.sinensis	7.0	0.006	3.32	**0.003**	5.0	0.9	2.15	0.070	3.0	1.976×10^{12}	1.21	0.316	1.9	134.5	11.54	**<0.001**
	P.damicornis	7.0	0.004	1.39	0.25	5	0.298	1.882	0.143	1.1	4.793×10^{12}	13.71	**0.017**	3.0	0.7	4.87	**0.019**
Site*Time	*M.ampliata*	7.9	0.017	6.21	**<0.001**	6.2	8.0	5.44	**<0.001**	4.2	2.63×10^{12}	3.50	**0.013**	2.5	45.4	1.53	0.230
	P.speciosa	7.5	0.016	7.73	**<0.001**	7.1	3.3	1.56	0.159	2.5	7.76×10^{12}	0.86	0.454	3.5	27.2	2.09	0.107
	P.sinensis	14.0	0.004	2.23	**0.012**	10.0	9.1	2.24	0.055	6.0	2.55×10^{12}	1.57	0.179	3.8	15.2	1.31	0.291
	P.damicornis	7.0	0.007	2.71	**0.028**	5.0	0.1	0.43	0.834	1.1	1.097×10^{12}	3.14	0.065	3.0	0.3	1.86	0.190

Table 2: Post hoc analysis using Bonferroni on untransformed data (n=9). Significant results (in bold) indicate that there is a significant difference in coral condition among sites.

Species	Site	Yield			Growth rates			Symbiont density			Chlorophyll *a*		
		Hantu	**Kusu**	**Labrador**	**Hantu**	**Kusu**	**Labrador**	**Hantu**	**Kusu**	**Labrador**	**Hantu**	**Kusu**	**Labrador**
M.ampliata	**Hantu**		0.115	**<0.001**		0.392	0.116		1.000	1.000		1.000	1.000
	Kusu	0.115		**0.014**	0.392		1.000	1.000		0.275	1.000		1.000
	Labrador	**<0.001**	**0.014**		0.116	1.000		1.000	0.275		1.000	1.000	
P.speciosa	**Hantu**	**-**	**0.365**	**<0.001**		1.000	1.000		0.856	1.000		1.000	1.000
	Kusu	**0.365**	**-**	**<0.001**	1.000		1.000	0.856		0.438	1.000		1.000
	Labrador	**<0.001**	**<0.001**		1.000	1.000		1.000	0.438		1.000	1.000	
P.sinensis	**Hantu**		1.000	0.654		1.000	1.000		1.000	0.327		1.000	1.000
	Kusu	1.000		1.000	1.000		0.714	1.000		0.766	1.000		1.000
	Labrador	0.654	1.000		0.714	1.000		0.327	0.766		1.000	1.000	
P.damicornis	**Hantu**			**0.022**			0.15			0.289			0.193
	Labrador	**0.022**			0.15			0.289			0.193		

Table 3: Results of the PERMANOVA main test. Environmental variables (chla = chlorophyll *a*, grain = grain size, PAR = light levels, SAR = sediment accumulation rate, SSC = suspended sediment concentration, SST = sea surface temperature, WQI = water quality index) were added stepwise into a Distance Linear Model to find the best combination of variables that explained the most amount of variation in coral condition across all three sites.

Species	**Variable**	**AIC**	**SS**	**Pseudo-F**	***p* value**	**% variation explained**
M.ampliata	+ Grain	53.345	245	6.19	**0.01**	
	+ Chla	50.04	149	5.06	**0.02**	
	+ PAR	50.03	43	1.54	0.26	
	+ WQI	49.4	48	1.86	0.20	67.6
P.speciosa	+ PAR	53.4	150	3.78	**0.04**	
	+ SSC	51.8	109	3.27	0.07	
	+ Grain	51.1	64	2.11	0.17	51.6
P.sinensis	- Grain	62.5	13	0.18	0.75	
	- Chla	61	16	0.25	0.71	
	-SAR	59.5	16	0.27	0.69	
	- SSC	58.8	46	0.87	0.41	38.5
P.damicornis	+ Temp	49.9	182	3	0.08	
	+ SAR	43.9	198	4.58	**0.03**	
	+ Chla	36.9	194	8.92	**0.02**	
	+ Grain	36.6	28	1.36	0.36	82.9

Table 4: Comparison of guidelines from three studies (ASEAN guidelines, ANZECC guidelines, Moss et al., 2005) together with this studies water quality recommendations for coral growth.

	RECOMMENDATIONS				**SINGAPORE WATER QUALITY STATUS**			
	ANZECC (2000) For inshore tropical waters	**Moss et al., 2005** For inshore waters	**ASEAN (2002)** For aquatic life protection	**This study** For coral growth	**Typical value**	**Maximum value**	**Status**	**Concern**
Chlorophyll *a* (μg l^{-1})	0.7 to 1.4	0.6		1 to 1.5	1 to 2	3.2	Limit exceeded	Medium
Ammonium (μg l^{-1})	1 to 10		70	20 [B]	<20	120	Limit exceeded	High
Nitrate (μg l^{-1})	2 to 8[A]		60	100	50 to 200	280	Limit exceeded	High
TN (μg l^{-1})	100	145-155		175	150 to 250	360	Limit exceeded	Low
Phosphate (μg l^{-1})	5	3 to 8	15	20	<30	45	Limit exceeded	High
TP (μg l^{-1})	15	15 to 20		15	<20	43	Limit exceeded	Low
Turbidity (NTU)	1 to 20			5 to 10	<5	20[D]	Limit exceeded[D]	Medium
Aluminium (μg l^{-1})	ID				<200	700		
Silver (μg l^{-1})	0.8 to 2.6[C]				<0.5	2	Within limits	None
Cadmium (μg l^{-1})	0.7 to 3[C]		10		<0.2	0.5	Within limits	None
Copper (μg l^{-1})	0.3 to 8[C]		8		<4	12	Limit exceeded	Low
Iron (μg l^{-1})	ID				<100	350		
Nickel (μg l^{-1})	7 to 560[C]				<4	16	Within limits	None
Lead (μg l^{-1})	2.2 to 12[C]		8.5		<1	6	Within limits	None
Zinc (μg l^{-1})	7 to 43[C]				10	35	Within limits	None

[A] Nitrate + Nitrite
[B] Ammonia
[C] Lower limit to protect 99% of species and upper limit to protect 80% of species
[D] Note that these data are from water samples. Authors have YSI data that indicate that turbidity can reach >150 mg L^{-1}
[ID] Insufficient data

Figure legends

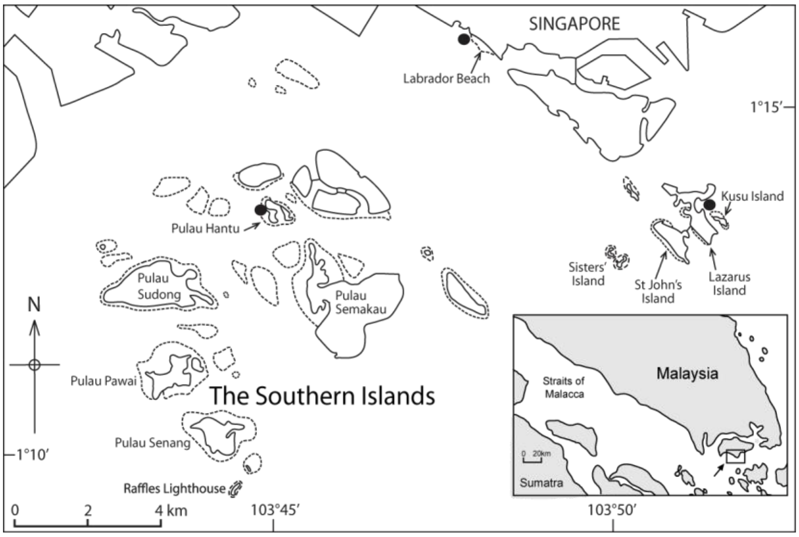

Figure 1: Map of the region.

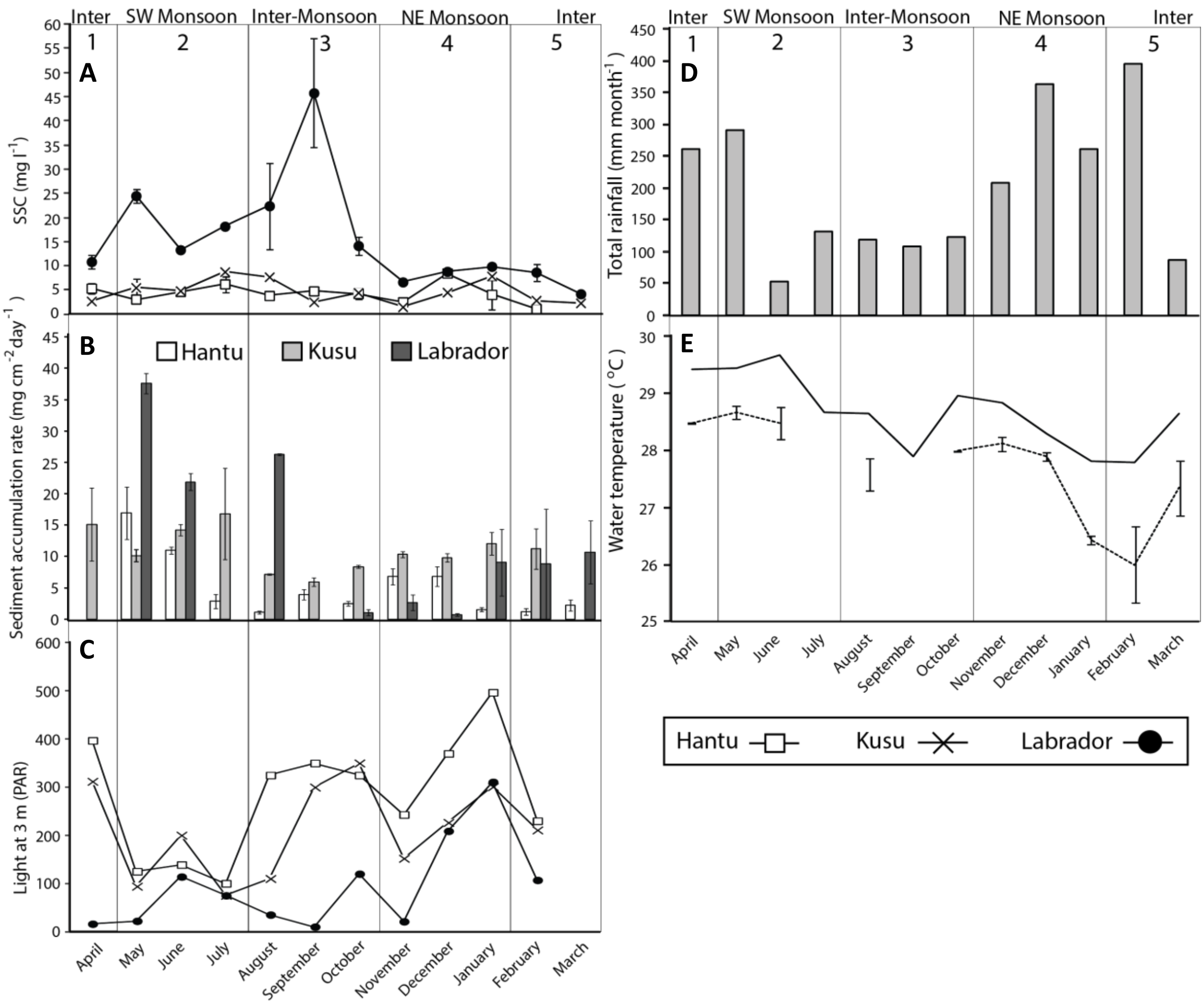

Figure 2: Monthly variations in A. suspended sediment concentration (SSC), B. sediment accumulation, C. light, D. total rainfall (data supplied by the Singapore Meteorological Services) and E. Water temperature at 3 m (dotted line) and at the surface (continuous line; data supplied by the Singapore Meteorological Services) over one year at Pulau Hantu, Kusu Island and Labrador Park. The south-westerly monsoon falls in season 2 and the north-easterly monsoon falls in season 4.

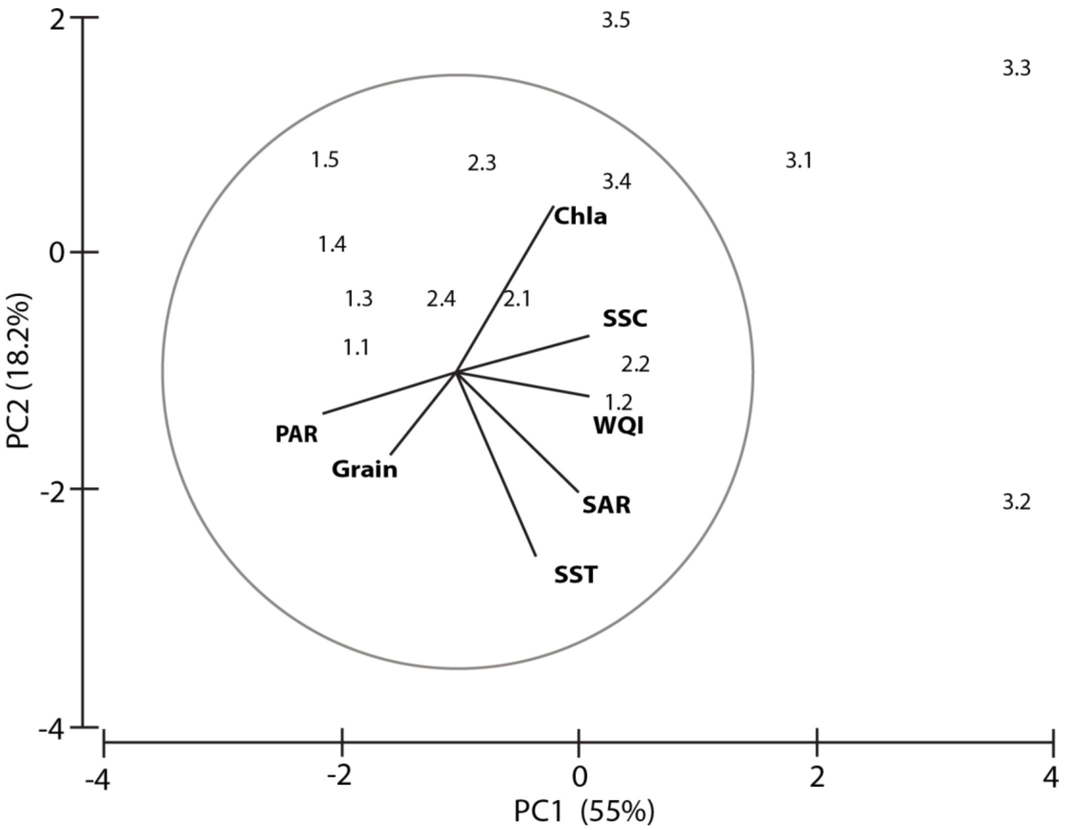

Figure 3: Principle components analysis of water quality variables sampled over one year at Hantu, Kusu Island and Labrador Park (chla = chlorophyll *a*, grain = grain size, PAR = light levels, SAR = sediment accumulation rate, SSC = suspended sediment concentration, SST = sea surface temperature, WQI = water quality index). Numbers denote the site (1= Hantu, 2= Kusu Island, 3= Labrador Park) and sampling season (1= April 2012, 2= May-July 2012, 3=Aug-Oct 2012, 4= Nov – Jan 2013, 5= Feb-March 2013).

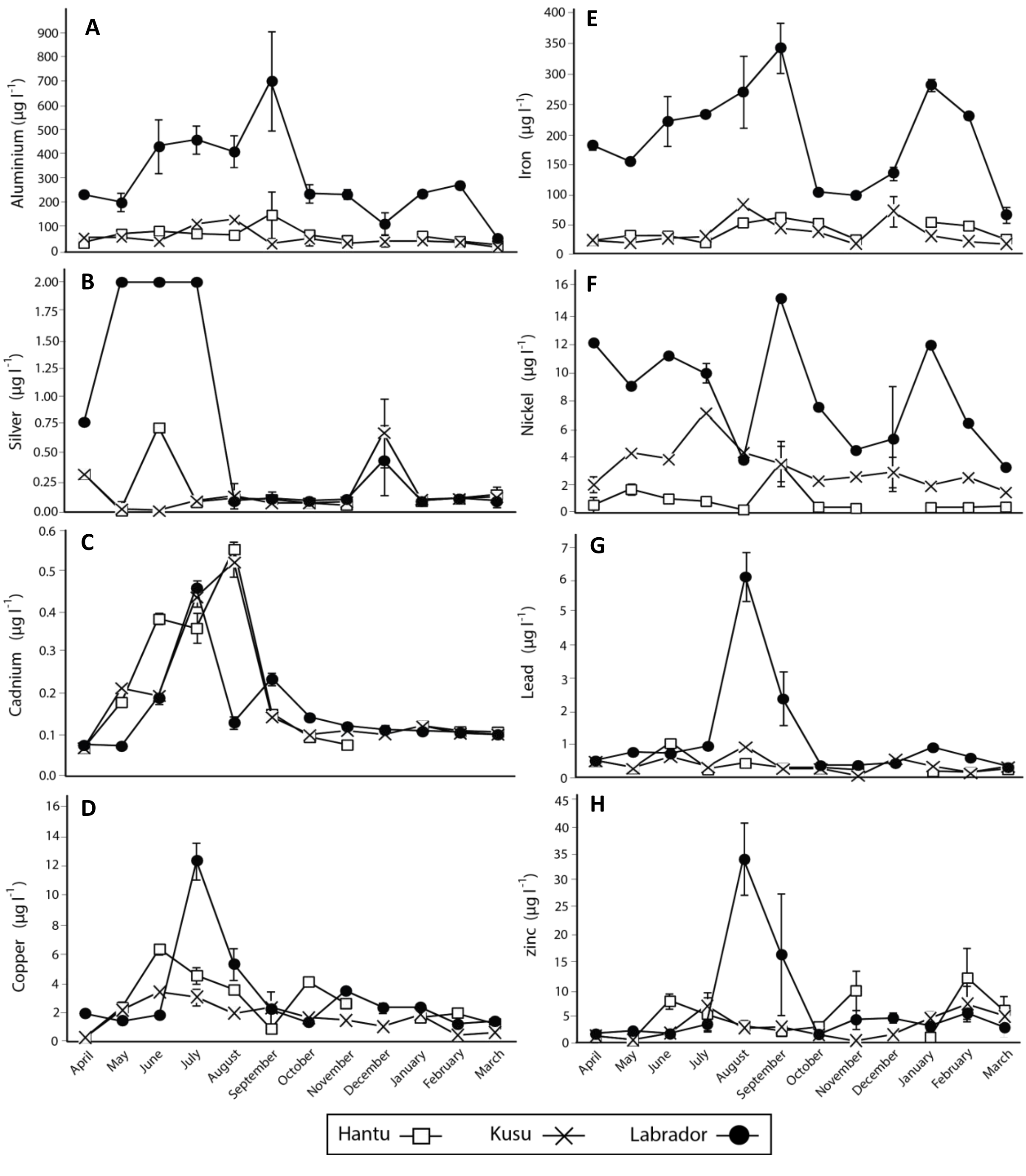

Figure 4: Monthly variations in trace metals over one year at Pulau Hantu, Kusu Island and Labrador Park. Error bars represent standard errors and n = 18. Water quality parameters included: A. aluminium B. silver C. cadmium D. copper E. iron F. nickel G. lead and H. zinc.

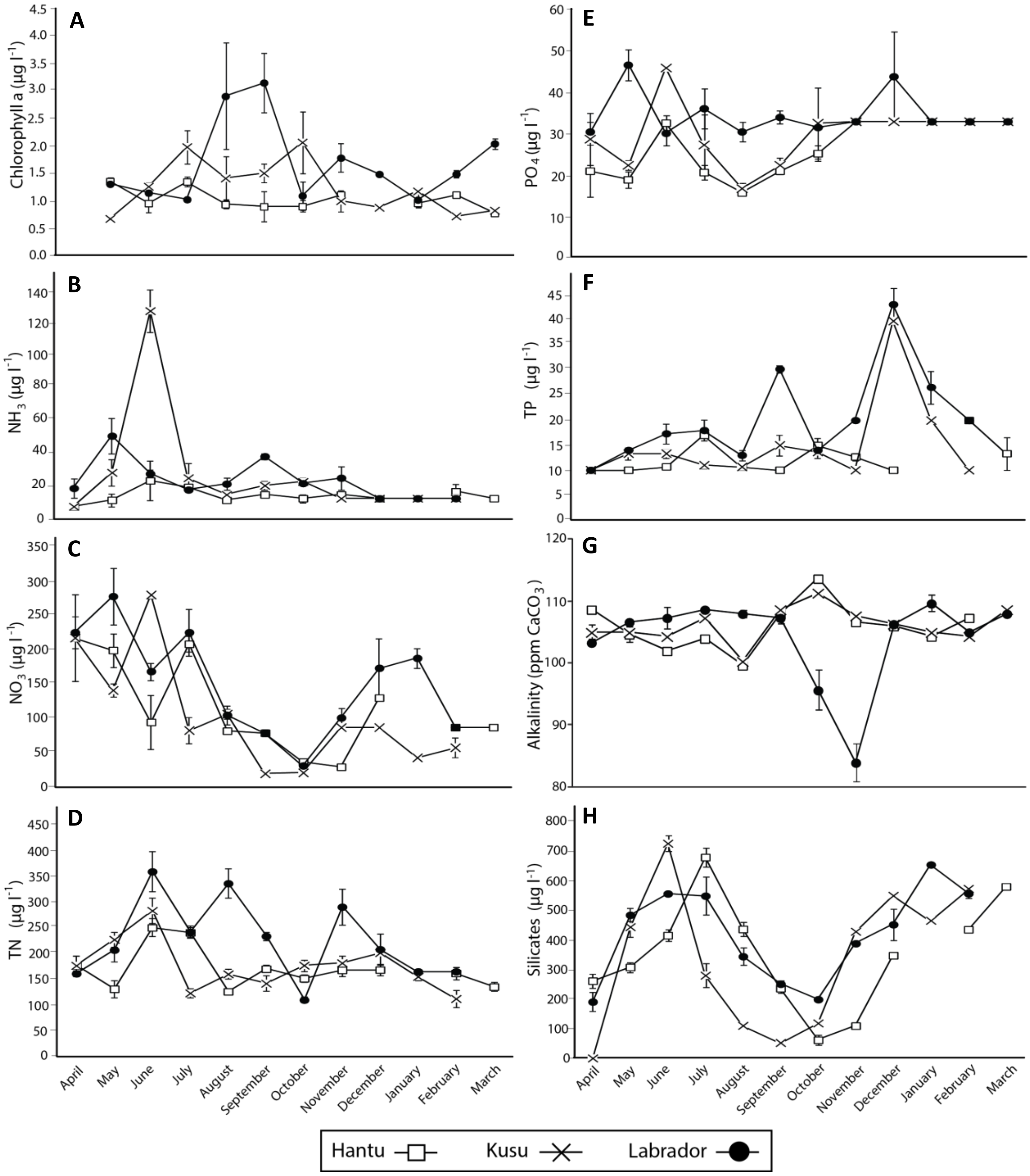

Figure 5: Monthly variations in water quality parameters over one year at Pulau Hantu, Kusu Island and Labrador Park. Error bars represent standard errors and n = 18. Water quality parameters included: A. Chlorophyll *a* B. Ammonia (NH_3) C. Nitrates (NO_3) D. Total Nitrogen (TN) E. Phosphates (PO_4) F. Total phosphates (TP) G. Alkalinity and H. Silicates.

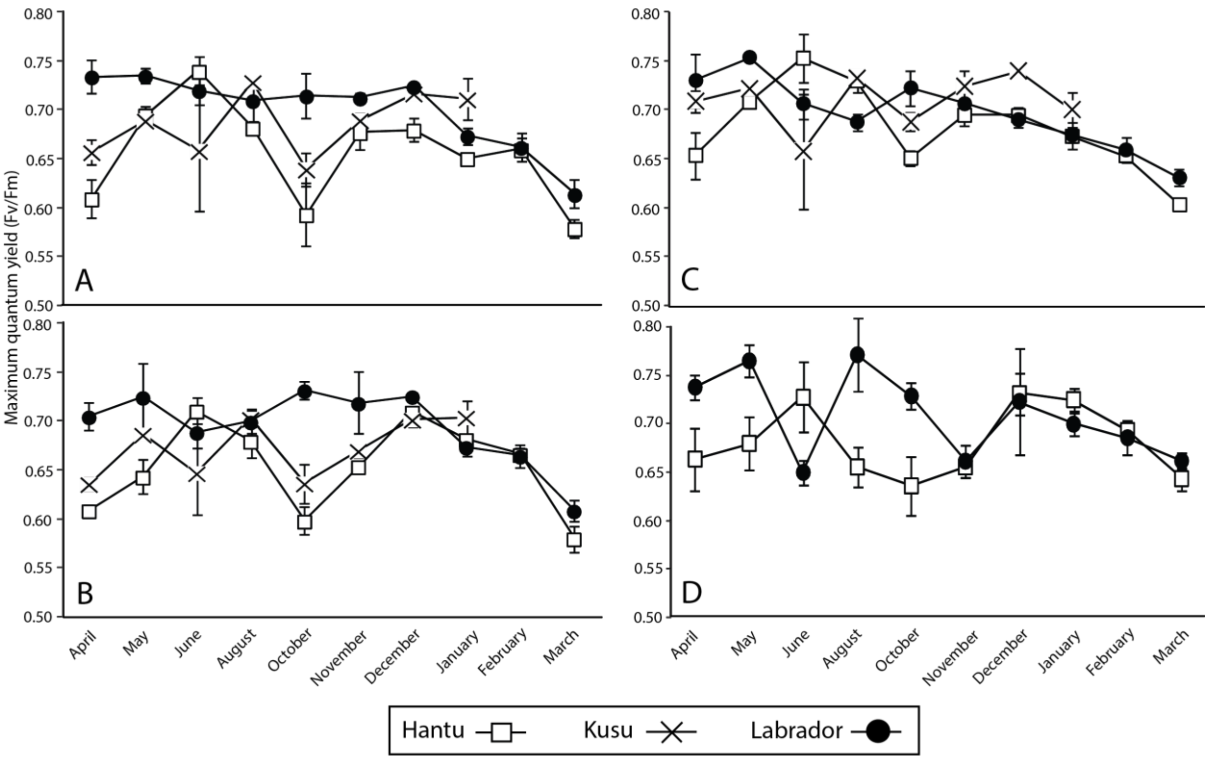

Figure 6: Maximum quantum yield (Fm/Fv) for A. *M.ampliata* B. *P.speciosa* C. *P.sinensis* and D. *P.damicornis.* Error bars represent standard errors and n = 27.

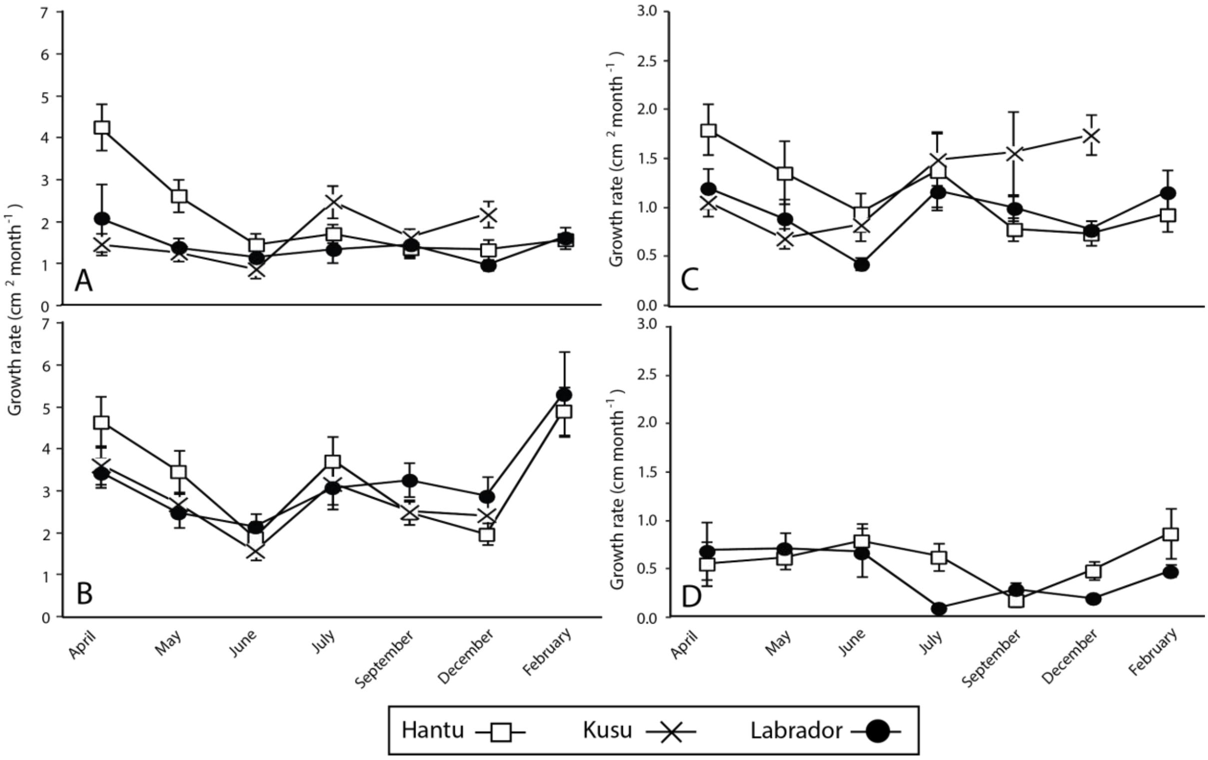

Figure 7: Growth rates for A. *M.ampliata* B. *P.speciosa* C. *P.sinensis* and D. *P.damicornis.* Error bars represent standard errors and n = 9. Please note that the growth rate for *P.damicornis* is in cm mo^{-1} whereas the growth rates for the other three coral species was in cm^2 mo^{-1}

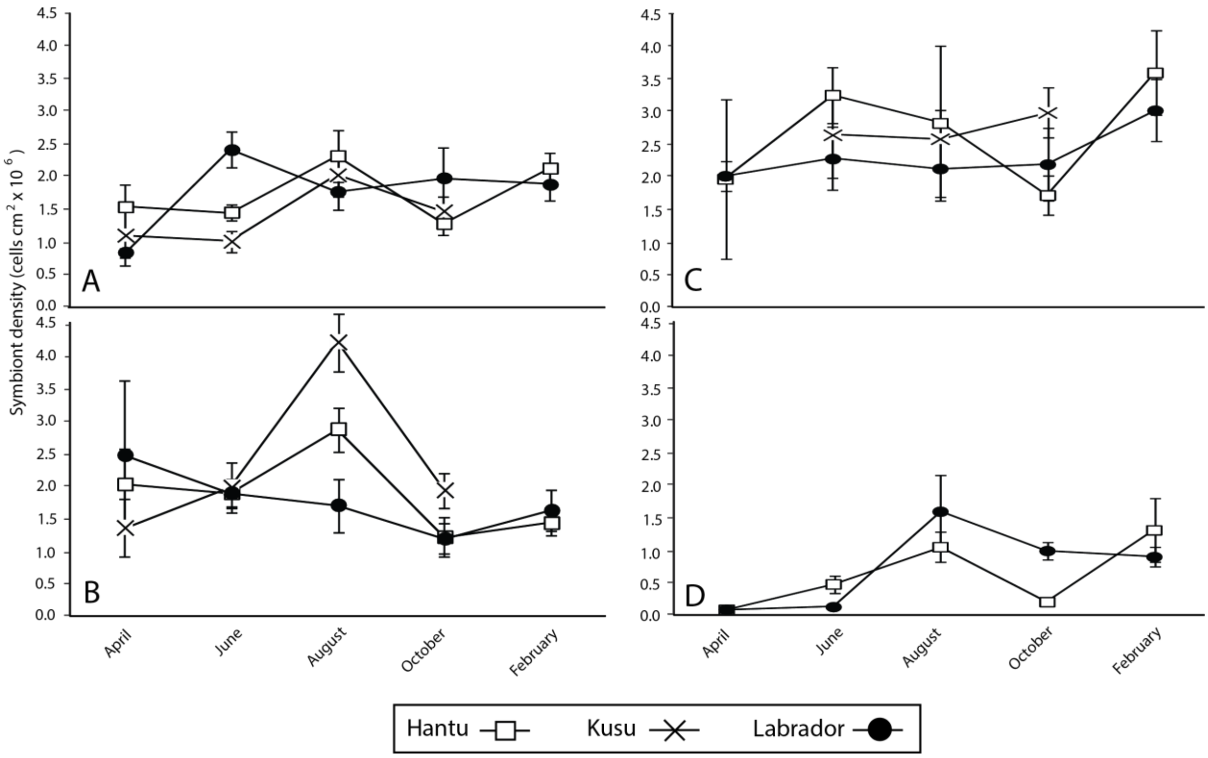

Figure 8: Symbiont density for A. *M.ampliata* B. *P.speciosa* C. *P.sinensis* and D. *P.damicornis*.. Error bars represent standard errors and *n* = 18.

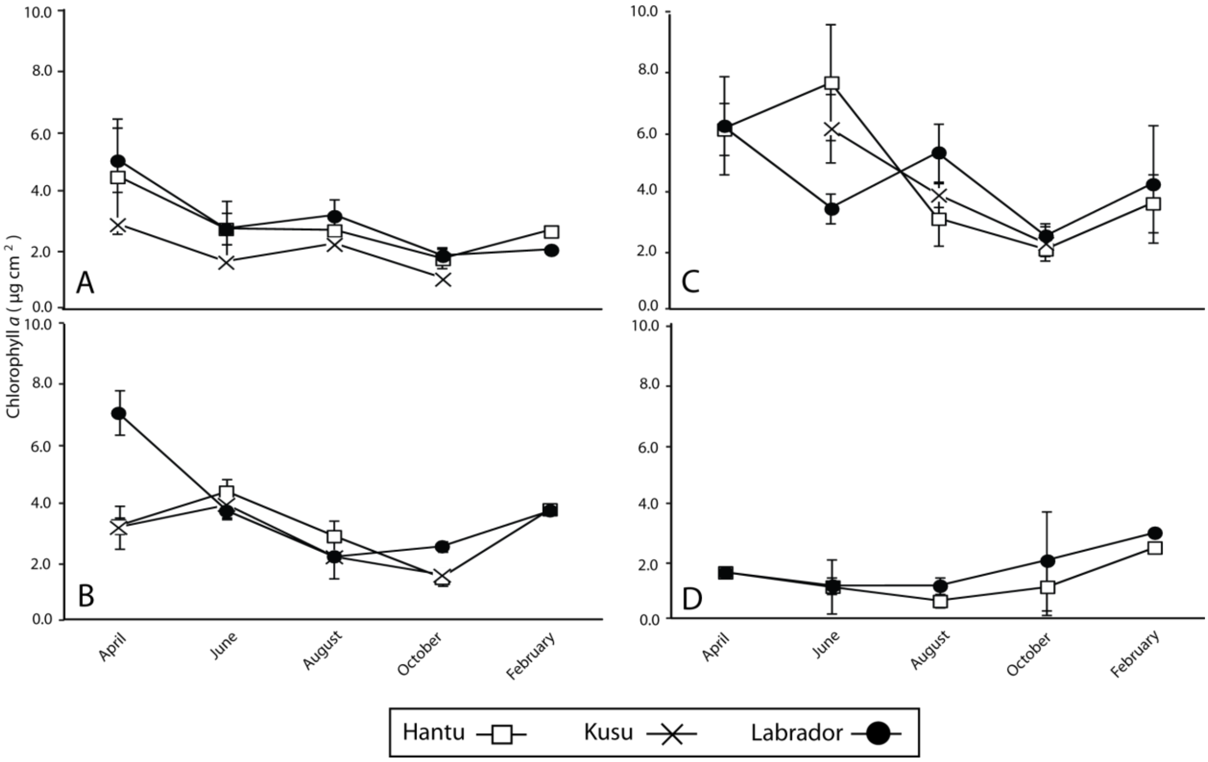

Figure 9: Chlorophyll *a* concentrations for A. *M.ampliata* B. *P.speciosa* C. *P.sinensis* and D. *P.damicornis*. Error bars represent standard errors and n = 18.

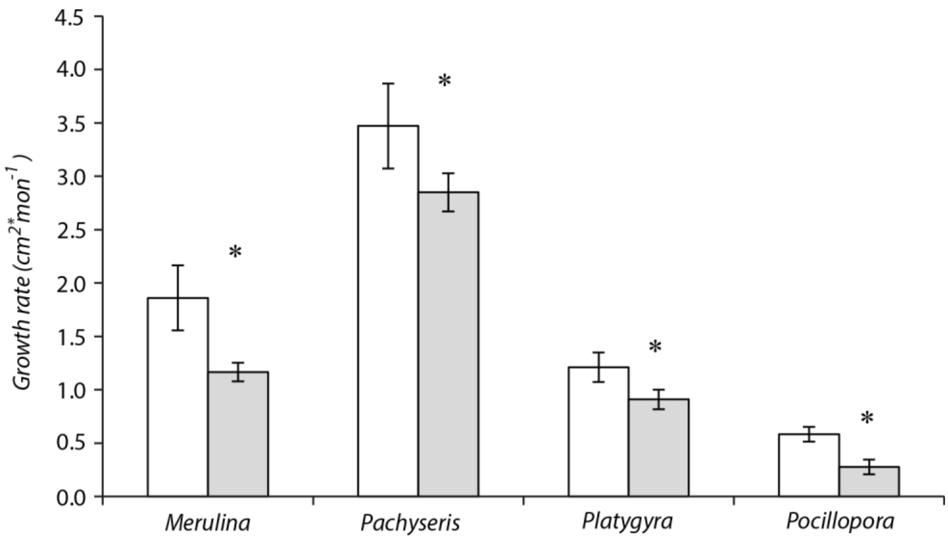

Figure 10: Mean coral growth rates for months characterised by improved WQI (<-0.1; white bars) and reduced WQI (>0.00; grey bars). Note that coral growth rates for *P.damicornis* is in cm mon^{-1}.